

First Cretaceous record of the gastropod *Exilia* (Neogastropoda: Ptychatractidae) from the northeastern Pacific

Richard L. Squires

Department of Geological Sciences
California State University
Northridge, CA 91330–8266 USA
and
Invertebrate Paleontology¹
Natural History Museum of Los Angeles County
Los Angeles, CA 90007 USA
richard.squires@csun.edu

Mary S. Stecheson

224N. Alta Vista Ave.
Monrovia, CA 91016 USA
stecheson@earthlink.net

ABSTRACT

A new species of the ptychatractid neogastropod, *Exilia stechesonae* Squires, is described from Upper Cretaceous (upper lower to lower upper Campanian) strata in southern California. It is found predominantly in the lower and middle parts of the Chatsworth Formation in the Simi Hills, Los Angeles and Ventura counties, and in the Pleasants Sandstone Member of the Williams Formation in the Santa Ana Mountains, Orange County. Specimens lived at shelfal depths and were subject to post-mortem transport into deeper waters. The new species is first Cretaceous record of *Exilia* Conrad, 1860 in the northeast Pacific.

Additional Keywords: Dayton Canyon, Bee Canyon, *Paleofusimitra*

INTRODUCTION

Neogastropods, which are among the geologically youngest of all the gastropod groups, first appeared in the Cretaceous. Their increasing diversity, especially during the Late Cretaceous, is one of the major features of gastropod evolution (Sohl, 1987; Harasewych et al., 1997). According to Kantor (2002), one of the most primitive of the neogastropods is family Ptychatractidae Stimpson, 1865, whose fossil record is based predominantly on *Exilia* Conrad, 1860. The geologic range of *Exilia* is Late Cretaceous (Coniacian) to Holocene (Kantor et al., 2001). During the Maastrichtian, *Exilia* became more widespread globally, and this expansion continued into the early Cenozoic. Several Paleocene, Eocene, and early Oligocene *Exilia* species are present in the northeast Pacific (Bentson, 1940; Squires, 2003).

This present study concerns the recognition of a new species, *Exilia stechesonae* Squires, from shallow-marine Upper Cretaceous (Campanian) beds in the Chatsworth

and Williams formations in southern California (Figure 1). It is the first Cretaceous occurrence of *Exilia* in the northeast Pacific region. Additional significance of the new species is that it helps to better understand the early evolution of *Exilia*. **The senior author, Squires, is the sole author of this new species.**

MATERIALS AND METHODS

The new species is based on 40 specimens stored in the Invertebrate Paleontology Collection of the Natural History Museum of Los Angeles County. Details about the localities of the new species are given in Appendix 1. Cleaning of apertures and cutting of a few longitudinal cross sections were done mostly by others using a hand-held, high-speed drill with diamond-coated drilling wheels. The classification system of Bouchet (2014) is followed here, but the “subclass” and “order” categories remain in a state of flux. Morphologic terms are from Cox (1960a).

Abbreviations used in the text are: CIT: California Institute of Technology, Pasadena (collection now stored at LACMIP); CSUN: California State University, Northridge (collection now stored at LACMIP); LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology; UCLA: University of California at Los Angeles (collection now stored at LACMIP); VIPM: Vancouver Island Paleontological Museum, Qualicum Beach, British Columbia, Canada.

STRATIGRAPHY, DEPOSITIONAL ENVIRONMENTS, AND AGES

The geology and paleontology of the Chatsworth Formation are discussed in Squires et al. (1981), Link et al. (1984), and Stecheson (2004). Inventories of the molluscan fossils in this formation are in Popenoe (1942) and

¹ Research Associate.

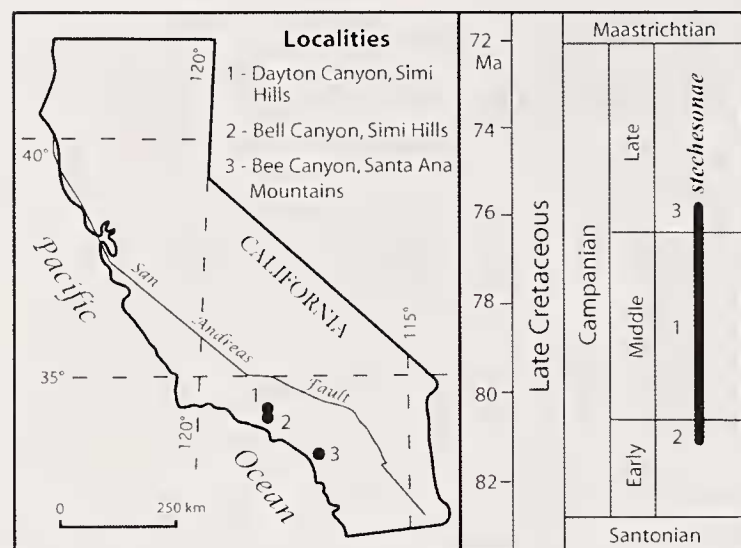


Figure 1. Index map and chronostratigraphic diagram. Geologic ages from Gradstein et al. (2012).

Saul and Alderson (1981). Stecheson's (2004) study was the first comprehensive systematic paleontologic study done on the gastropods of the Chatsworth Formation in the Bell Canyon and Dayton Canyon areas in the southeastern part of the Simi Hills (Fig. 1). Faulting and discontinuous bedding obscure the stratigraphic relationships between the Bell Canyon and Dayton Canyon fossil localities, but the Bell Canyon beds are slightly older than the Dayton Canyon beds (Stecheson, 2004). The base of the Chatsworth Formation is not exposed (Link et al., 1984).

Only a few specimens of the new gastropod were found at LACMIP loc. 10710 in the lower 10 m of the lower part of the stratigraphic section of the Chatsworth Formation exposed in Bell Canyon. The fossils at this locality are concentrated in lens-shaped beds of calcareous sandstone that accumulated as channelized deposits in slope and submarine mid-fan facies (Link et al., 1984). Based on the concurrent ranges of the gastropods *Volutoderma averillii* and *Lysis suciensis*, the rocks at this locality are of late early Campanian age (Saul and Squires, 2008a, 2008b).

Nearly all of the fossils of the new species were found at its type locality (LACMIP loc. 10715). This locality, which is in the middle part of the Chatsworth Formation in Dayton Canyon, Los Angeles County, southern California, is approximately 4 km northeast of Bell Canyon. Locality 10715 was described by Squires and Saul (1981) as a 1.8 m thick and 15 m long, highly fossiliferous lens. Fossils make up about 80 percent of the lens. In addition to gastropods, there are bivalves, ammonites, nautiloids, and shark teeth. The fossils were likely swept from various depths on a shelf by channelized debris flows, then transported and concentrated on the adjacent slope (Link, 1981; Link et al., 1984). The rock type at the locality is fine- to medium-grained sandstone with scattered rip-up clasts. The poorly sorted fossil remains are stratified. Although most of the fossils are fragmental, they are not worn or abraded (Squires and Saul, 1981). Based on the presence of the gastropods *Volutoderma angelica*, *V. blakei*, *V. santana*, and *V. elderi*, the rocks at this locality are of middle Campanian age (Saul and Squires, 2008a).

Nearly all the specimens from the Williams Formation are poorly preserved fragments, except for a specimen (Fig. 8) found at LACMIP loc. 42320 near the mouth of Bee Canyon, southern California (Fig. 1). This locality is in a fault-bounded inlier of Upper Cretaceous rocks mapped by Schoellhamer et al. (1981) and referred to by Saul and Squires (2008a) as the Pleasants Sandstone Member. These rocks are shallow-marine shelfal deposits containing the gastropod *Volutoderma? antherana*, which is indicative of early late Campanian age (Saul and Squires, 2008a).

During the Campanian, the west coast of the United States was part of the "Northeast Pacific Subprovince" of Kauffman (1973: fig. 1), which, in turn, was part of his "North Temperate Realm." This subprovince had warm-temperate coastal conditions (Kiel, 2002: fig. 2; Saul and Squires, 2008a).

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

"Subclass" Caenogastropoda Cox, 1960b

"Order" Neogastropoda Wenz, 1938

Superfamily Turbinelloidea Rafinesque, 1815

Family Ptychatractidae Stimpson, 1865

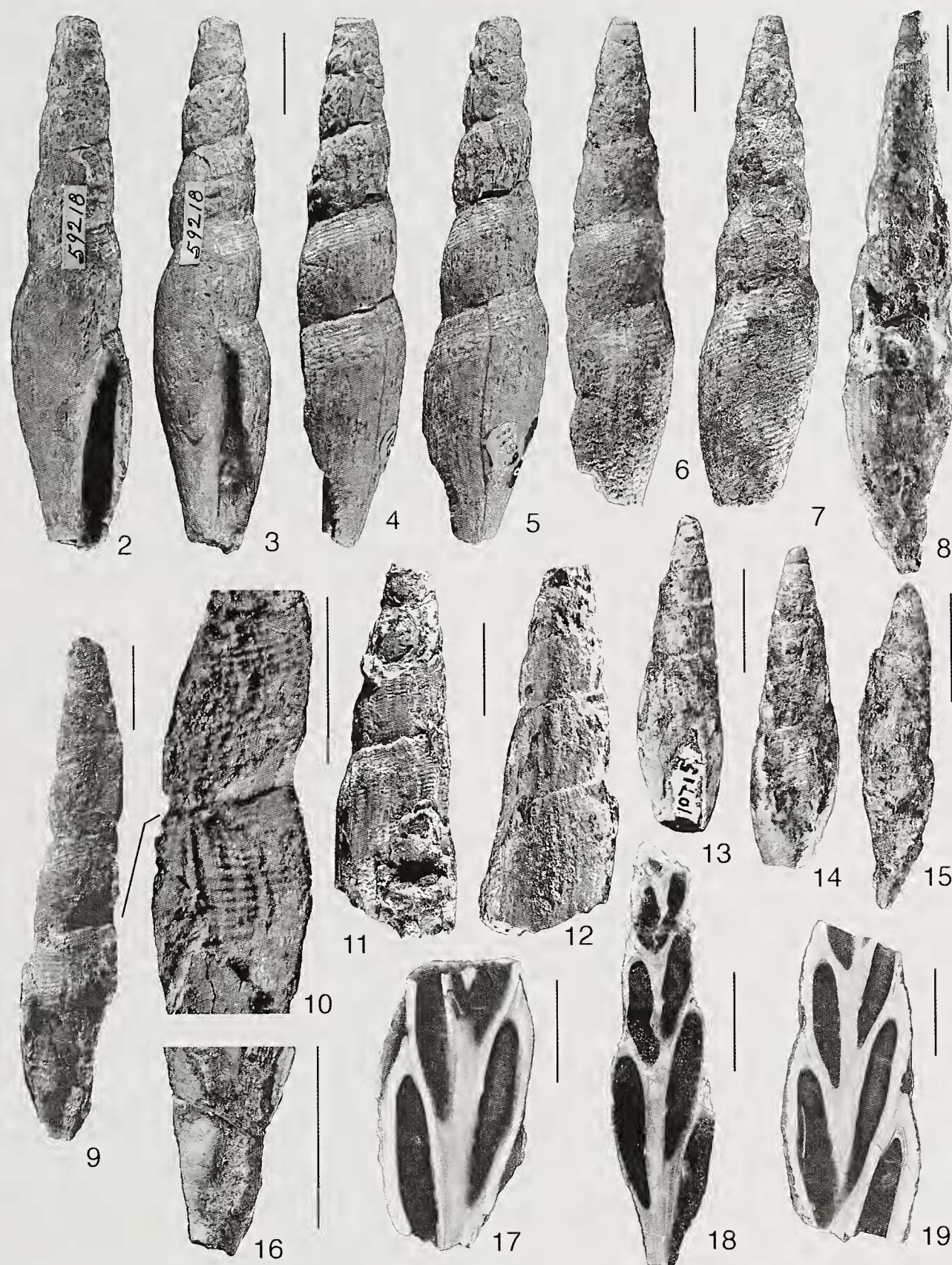
[= Graphidulidae Stephenson, 1941]

Discussion: Stimpson (1865: 59) named the family Ptychatractidae to accommodate his new genus *Ptychatractus*, a deep water modern-day gastropod from Maine and Nova Scotia. He did not comment on the higher taxonomic relationships of his family, which has an ongoing unsettled and inconsistent classification history. Nielsen (2005) provided a succinct discussion of this complicated history. Kantor et al. (2001) discussed the synonymy of genus *Exilia* in detail. Classification adjustments continue to modern day, as evidenced by recent anatomical and molecular phylogeny studies done by Fedosov et al. (2017), which indicate close relationships among modern costellariids (ribbed miters), ptychatractids, and volutomitrids.

Genus *Exilia* Conrad, 1860

Type Species: *Exilia pergracilis* Conrad (1860, by monotypy; middle Paleocene ["Midway"]), Alabama, Mississippi, and Texas (Palmer and Brann, 1966; Toulmin, 1977).

Description: Shell approximately 10 to 101 mm height; most shells 15 to 55 mm height. Height/width ratio ranges from 3.2 to 5.3. Fusiform, long and narrow to moderately short and moderately wide. Spire high to, less commonly, short. On unbroken specimens, height of spire commonly greater than height of aperture. Spire outline evenly tapered or knobby/angularate. Spire (pleural) angle 13° to approximately 30°. Protoconch smooth, 0.8 to 3 whorls (paucispiral or multispiral), depending on larval development. Teleoconch with up to approximately eight or nine



Figures 2–19. *Exilia stechesonae* new species Squires, LACMIP loc. 10715, southern California, Chatsworth Formation, unless otherwise indicated. **2–5.** Holotype LACMIP 10496. **2.** Apertural view. **3.** Apertural view, turned slightly to show columella interior. **4.** Right-lateral view. **5.** Abapertural view, showing growth line. **6–7.** Paratype LACMIP 14748. **6.** Right-lateral view. **7.** Abapertural view. **8.** Paratype LACMIP 14749, right-lateral view. **9–10.** Paratype LACMIP 14750, LACMIP loc. 42320, Pleasants Sandstone Member. **9.** Abapertural? view. **10.** Closeup of two whorls; crooked line denotes same juncture of two whorls in previous figure. **11–12.** Paratype LACMIP 14751, upper spire. **11.** Apertural view. **12.** Abapertural view. **13–14.** Paratype 14752. **13.** Apertural view. **14.** Abapertural view. **15.** Paratype 14753, LACMIP loc. 10710, left-lateral view showing upturned anterior end. **16.** Paratype LACMIP 14754, apertural view of anterior end. **17.** Paratype LACMIP 14755, longitudinal view of interior showing 1–2 plaits. **18.** Paratype LACMIP 14756, longitudinal view of interior showing 1–2 plaits. **19.** Paratype LACMIP 14757, longitudinal view of interior showing 1–2 plaits. Scale bars = 10 mm.

whorls, or, much less commonly, four to five whorls. Whorls convex (rarely somewhat flat-sided), with convexity weak to moderately strong; whorls can be angulate (rarely tabulate). Sculpture varies considerably in strength, from very weak to strong. Most shells with obvious sculpture (especially on spire), whereas some shells overall smooth-looking. Axial ribs weak to strong and commonly stronger than spiral sculpture. Axial ribs narrow to moderately wide in size and spacing; straight or curved, commonly elongate and extending from suture to suture, but not aligned with axial ribs on adjacent whorls. Axial ribs can be noded. Axial ribs common on spire and most of last whorl; or axial ribs only on upper spire. Spiral ribs very weak to strong, narrow to moderately wide, commonly closely spaced. Spiral ribs strongest on shoulder and neck but can be nearly obsolete on shoulder of last whorl. Cancellate sculpture moderately common. Aperture narrow to moderately wide, narrowly elongate. No anal sulcus. Outer lip thin and smooth. Columella callus slight, with zero or two to four concealed plaits of variable strength. Siphonal canal commonly long but can be relatively short (attenuated). Siphonal notch narrow to moderately narrow. Anterior end very rarely upturned slightly but untwisted (i.e., no siphonal fasciole). Operculum absent, or very small with subcentral nucleus, or medium sized with terminal nucleus. Growth line straight or inclined on spire whorls; slightly sinuous on last whorl, with deflections near suture, on angulation at periphery, and on neck (Bentson, 1940; Kantor et al. 2001; herein).

Geologic Age: Coniacian to Holocene (Kantor et al., 2001: fig. 5).

Discussion: *Exilia* has considerable variation in its spire angle, height/width ratio, morphology of the protoconch, relative strengths of the spiral and axial sculpture, and number and strength of the columellar plaits (Kantor et al., 2001: 84). To this list, we add shell size, spire height, and aperture width. Additionally, the narrow and elongate outline of many *Exilia* species resembles other gastropods belonging to other genera in various families (e.g., fusinids and fasciolarids) (Bentson, 1940: 204). Most of the extinct species of *Exilia* are based on only a few specimens although, in some cases, a substantial number (e.g., 20 to 40) of specimens is available. Specimens are commonly broken or poorly preserved.

Bentson (1940) reported on all the American and European species of *Exilia* and emphasized their morphology and stratigraphic distribution. Based on measurements given by Bentson (1940) and Kantor et al. (2001), Paleogene *Exilia* have the smallest shells of all the species of *Exilia*. Bentson (1940) also commented briefly on the biogeography and ecology of *Exilia*.

Kantor et al. (2001) used anatomical studies to significantly revise the systematics of this genus, synonymized many nominal genera with *Exilia*, provided useful digital images of some fossil and modern-day species, and commented on the biogeography and ecology of this genus. Cretaceous and early Paleogene *Exilia* lived in

upper and middle shelfal depths near the southern border of the "North Temperate Realm," and the first relatively deep water (lower shelf to bathyal) occurrences of this genus did not take place until the late Eocene. Today, the genus is confined to bathyal depths at tropical latitudes and in the New Zealand region (Kantor et al. 2001).

There has been confusion concerning *Exilia pergracilis* Conrad (the type species) and *Paleorhaphis pergracilis* Aldrich, (1886: 22, pl. 5, fig. 18) because of them having similar shells, the same species name (Bentson, 1940: 206–207), Paleogene age, and occurrence in Alabama. Kantor et al. (2001) regarded *Paleorhaphis* Stewart, 1927 as a junior synonym of *Exilia*, and, in so doing, made *Exilia pergracilis* (Aldrich, 1886) a secondary homonym of *Exilia pergracilis* Conrad, 1860.

Exilia stechosonae new species Squires (Figures 2–19)

Paleofusimitra n. sp. Saul and Alderson, 1981: 36, pl. 3, fig. 8; Squires and Saul, 1981: 131.

Graphidula? n. sp. Stecheson, 2004: 91–92, pl. 3, figs. 8, 9.

Diagnosis: *Exilia* with medium shell size, spire high with narrow spire angle (13° to 17°), teleoconch whorls (about seven) lowly convex to somewhat flattened, sculpture weak (can be missing on parts of penultimate and last whorls), axials widely spaced, spirals narrower and closely spaced, cancellate sculpture (minute) can be present, aperture narrow and slightly upturned (but untwisted) dorsally at its anterior end, columella with one or two very small concealed plaits spaced about 2.5 mm apart.

Description: Shell up to 78.2 mm height and 15.8 mm width (same specimen); height to width ratio approximately 4.5 (most complete specimen); fusiform. Spire high, spire whorls tall. Protoconch missing. Spire angle 13° (adult specimens) to 17° (juvenile specimens). Teleoconch up to approximately seven whorls (estimated maximum of eight teleoconch whorls). Whorls lowly convex (can be somewhat flattened). Suture impressed to indistinct, with or without shell material extending slightly over suture region. Sculpture overall weak, locally can be absent. Axial sculpture consisting of weak, widely to irregularly spaced narrow ribs, extending from suture to suture. Spiral sculpture consisting of weak, closely spaced narrow ribs present on most of teleoconch whorls (on some specimens spiral sculpture can be missing on anterior two-thirds of penultimate and last whorls). Cancellate sculpture (minute) can be present. Aperture narrow and slightly upturned (but untwisted) dorsally at its anterior end. Siphonal canal narrow, with siphonal notch very small and narrow. Inner lip (columellar lip) with light callus. Columella generally straight, with one or two very small concealed plaits, spaced about 2.5 mm apart, and with variation as to which one is stronger. Outer lip thin and smooth. Growth line slightly sinuous on last whorl; slightly prosocline near suture, very slightly and

broadly opisthocline across weak angulation on posterior third of last whorl; and slightly prosocline on neck.

Holotype: LACMIP 10496 [ex hypotype LACMIP 10496], height 66.5 mm (incomplete with uppermost spire and anterior end of aperture missing), width 14.6 mm (Figures 2–5).

Paratypes: LACMIP 14748–14757.

Type Locality: LACMIP 10715. See Squires (1981: insert) for the location of this locality plotted on a topographic base map.

Geologic Age: Late early to early late Campanian.

Distribution: UPPER LOWER CAMPANIAN: Chatsworth Formation, Bell Canyon, Simi Hills, Ventura Co., southern California. MIDDLE CAMPANIAN: Chatsworth Formation, upper Dayton Canyon, Simi Hills, Los Angeles Co., southern California. LOWER UPPER CAMPANIAN: Williams Formation, Pleasants Sandstone Member, near mouth of Bee Canyon, Santa Ana Mountains, Orange Co., southern California.

Etymology: The new species is named for Mary S. Stecheson, in recognition of her study of the systematic paleontology of the gastropod fauna of the Chatsworth Formation. **The senior author, Squires, is the sole author of this new species.**

Discussion: Forty specimens were examined: 38 from the Chatsworth Formation in Dayton Canyon; one specimen from the Chatsworth Formation in Bell Canyon; and one specimen from the Williams Formation (Pleasants Sandstone Member) in Bee Canyon. All the specimens are weathered, and the sculpture, especially the axial ribs, is commonly subdued as a result. All specimens are incomplete, most likely the result of damage during collecting. No specimens have the protoconch or uppermost spire present. The anterior tip of the shell is commonly also missing. About 16 Chatsworth Formation specimens have most of the aperture present. The somewhat crushed figured specimen (Figures 9, 10) from the Williams Formation has the best preservation of the details of the sculpture. A few of the specimens are steinkerns, and some have large portions of the shell missing. Although none of the specimens are in the best possible state of preservation, the preservation is good enough to show the most important morphological characteristics.

The largest specimen (Figure 8) of the new species is from Dayton Canyon and is 78.2 mm height (incomplete), 17.4 mm width, with an estimated complete height of 80 mm. The new species is one of the tallest Late Cretaceous ptychatractids. *Exilia melanopsis* (Conrad, 1860) from the Late Cretaceous (Maastrichtian) of Tennessee is approximately the same height as *E. stechesonae*. In comparison, most other species (e.g., those illustrated by Kantor et al., 2001) of Late Cretaceous *Exilia* are small to moderate in size (19 to 48 mm height).

Exilia stechesonae with its narrow spire angle, lowly convex whorls, weaker sculpture, and narrow aperture differs from most other species of *Exilia*. The new species is somewhat similar to some *Exilia* in terms of the height to width ratio of approximately 4.5, relatively narrow spiral angle, lowly convex whorls, subdued sculpture, and a narrow aperture. An example of one of these somewhat similar species is *Exilia clarki* Benton (1940: 215–216, pl. 2, figs. 2, 3, 8, 12, 15, 17, 19, 20) from the upper middle Eocene Cowlitz Formation in southwestern Washington. The new species differs by having a much larger shell, slightly upturned anterior end, and much less prominent axial ribs. The degree of the prominence of the axial ribs on the new species, however, is difficult to assess because of the effects of weathering.

Saul and Alderson (1981) regarded the new gastropod described here as belonging to genus *Paleofusimitra* Sohl, 1963, which they questionably assigned to family Mitridae Swainson, 1831. *Paleofusimitra* is known with certainty only from upper Campanian strata in the Ripley Formation in Mississippi, Alabama, and Georgia (Sohl, 1963, 1964). Sohl (1963, 1964) and Cernohorsky (1970: 26, 39, pl. 4, figs. 6, 7) assigned *Paleofusimitra* to the mitrids. Cernohorsky (1970: 26) mentioned, furthermore, that *Paleofusimitra* is one of the earliest mitrids retaining some of the fascioliid features. Cernohorsky (1976: 512, pl. 462) reported that if *Paleofusimitra* is a mitrid, it is the most primitive one and retained strong fascioliid features (e.g., placement and number of the columellar folds). The new species differs from *Paleofusimitra* by having a much larger size, a narrower pleural angle, narrower posterior part of the last whorl, narrower anterior part of the aperture, presence of axial ribs, more numerous and more closely spaced spiral ribs near suture, wider range of number of plaits, and absence of a slight siphonal fasciole.

The new species resembles superficially specimen VIPM 052 of the so-called *Nonacteonina* sp. of Ludvigsen and Beard (1994: 95, fig. 60, in part; Ludvigsen and Beard, 1997: 115, fig. 71, in part) from the Northumberland Formation at Collishaw Point, north end of Hornby Island, off the east coast of Vancouver Island, British Columbia, Canada. Katnick and Mustard (2003) assigned the rocks at Collishaw Point to the upper Campanian Northumberland Formation. The aperture of specimen VIPM 052 is not present. The new species differs by having a slightly wider spiral angle (13° to 17°, rather than 8° to 11°), less convex whorls, presence of axial ribs, and a less prosocline growth line near the suture.

ACKNOWLEDGMENTS

Lindsey T. Groves (LACM Malacology) and Steffen Kiel (Naturhistoriska Riskmuseet, Department of Paleobiology, Stockholm) provided key molluscan references. LouElla Saul (LACMIP) cleaned the holotype. Mark A. Roeder (Department of Paleontology, San Diego Natural History Museum) provided detailed locality information about the Bee Canyon specimen. The Transportation Corridor Agency funded the paleo-monitoring of the Bee Canyon

area. Raymond Graham (Victoria, British Columbia) provided stratigraphic and locality data concerning specimen VIPM 052 and also took digital images of this specimen for comparative purposes. Lindsey T. Groves and an anonymous person critically reviewed the manuscript and gave valuable comments.

LITERATURE CITED

- Aldrich, T.H. 1886. Preliminary report on the Tertiary fossils of Alabama and Mississippi. Geological Survey of Alabama Bulletin 1: 15–60.
- Bentson, H. 1940. A systematic study of the fossil gastropod *Exilia*. University of California Publications Bulletin of the Department of Geological Sciences 25: 199–238.
- Bouchet, P. 2014. World register of marine species, accessible at <<http://www.marinespecies.org>>
- Cernohorsky, W.O. 1970. Systematics of the families Mitridae & Volutomitridae (Mollusca: Gastropoda). Bulletin of the Auckland Institute and Museum 8: 1–190.
- Cernohorsky, W.O. 1976. The Mitridae of the world. Part 1. The subfamily Mitrinae. Indo-Pacific Mollusca 3: 273–528.
- Conrad, T.A. 1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Journal of Philadelphia Academy of Natural Sciences 2: 279–296.
- Cox, L.R. 1960a. Morphology of hard parts. In: Moore, R. C. (ed.) Treatise on Invertebrate Paleontology, Part 1, Mollusca 1. Geological Society of America and University of Kansas Press, pp. 1106–1135.
- Cox, L.R. 1960b. Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London 33: 239–261.
- Cuvier, G.L.C. 1797. Tableau élémentaire de l'histoire naturelle des animaux [des mollusques]. Baudouin, Paris, 710 pp.
- Fedosov, A., N. Puillandre, and P. Bouchet. 2017. Phylogeny, systematics, and evolution of the family Costellariidae (Gastropoda: Neogastropoda). Zoological Journal of the Linnean Society 179: 541–626.
- Gradstein, F.M., J. Ogg, M.D. Schmitz, and G.M. Ogg. 2012. The geologic time scale 2012. Two-volume set. Elsevier, Amsterdam, 1144 pp.
- Harasewych, M.G., S.L. Adamkewicz, J.A. Blake, D. Saudek, T. Spriggs, and C.J. Bult. 1997. Neogastropod phylogeny: A molecular perspective. Journal of Molluscan Studies 63: 327–351.
- Kantor, Y.I. 2002. Morphological prerequisites for understanding neogastropod phylogeny. Bollettino Malacologica, Supplemento 4, Roma, pp. 161–174.
- Kantor, Y.I., P. Bouchet, and A. Oleinik. 2001. A revision of the Recent species of *Exilia*, formerly *Benthovoluta* (Gastropoda: Turbinellidae). Ruthenica 11: 81–136.
- Katnick, D.C. and P.S. Mustard. 2003. Geology of Denman and Hornby Islands, British Columbia: Implications for Nanaimo Basin evolution and formal definition of the Goeffrey and Spray formations, Upper Cretaceous Nanaimo Group. Canadian Journal of Earth Sciences 40: 375–393.
- Kauffman, E.G. 1973. Cretaceous Bivalvia. In: Hallam, A. (ed.), Atlas of palaeobiogeography. Elsevier Scientific Publishing Company, Amsterdam: 353–383.
- Kiel, S. 2002. Notes on the biogeography of Campanian-Maastrichtian gastropods. In: Wagreich, W. (ed.), Aspects of Cretaceous stratigraphy and palaeobiogeography. Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommissionen, Vol. 15, pp. 109–127.
- Link, M.H. 1981. Sand-rich turbidite facies of the Upper Cretaceous Chatsworth Formation, Simi Hills, California. In: Link, M. H., R. L. Squires, and I.P. Colburn (eds). Simi Hills Cretaceous turbidites, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists Fall Field Trip Guidebook, Los Angeles, California: 63–70.
- Link, M. H., R.L. Squires, and I.P. Colburn. 1984. Slope and deep-sea fan facies and paleogeography of Upper Cretaceous Chatsworth Formation, Simi Hills, California. American Association of Petroleum Geologists Bulletin 68: 850–873.
- Ludvigsen, R. and G. Beard. 1994. West coast fossils. A guide to the ancient life of Vancouver Island. Whitecap Books, Vancouver, 194 pp.
- Ludvigsen, R. and G. Beard. 1997. West coast fossils. A guide to the ancient life of Vancouver Island. 2nd ed. Harbour Publishing, Madeira Park, Canada, 216 pp.
- Nielsen, S.N. 2005. *Exilia alanbeui*, a new species from the Neogene of central Chile: The first record of *Exilia* (Gastropoda: Ptychatactidae) from South America. The Nautilus 119: 153–156.
- Palmer, K.V.W. and D.C. Brann. 1966. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part 2. Bulletins of American Paleontology 48: 471–1057.
- Popenoe, W.P. 1942. Upper Cretaceous formations and faunas of southern California. American Association of Petroleum Geologists Bulletin 26: 162–187.
- Rafinesque, C.S. 1815. Analyse de la nature, ou tableau de l'univers et des corps organisés. Barravecchia, Palermo, 224 pp.
- Saul, L.R. and J.M. Alderson. 1981. Late Cretaceous Mollusca of the Simi Hills: An introduction. In: Link, M.H., R.L. Squires, and I.P. Colburn (eds). Simi Hills Cretaceous turbidites, southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists Fall Field Trip Guidebook. Los Angeles, California: 29–42.
- Saul, L.R. and R.L. Squires. 2008a. Volutoderminae (Gastropoda: Volutidae) of Coniacian through Maastrichtian age from the North American Pacific slope. Journal of Paleontology 82: 213–237.
- Saul, L.R. and R.L. Squires. 2008b. Cretaceous trichotropid gastropods from the Pacific slope of North America: Possible pathways to calyptraeid morphology. The Nautilus 122: 115–142.
- Schoellhamer, J.E., J.G. Vedder, R.F. Yerkes, and D.M. Kinney. 1981. Geology of the northern Santa Ana Mountains, California. U. S. Geological Survey Professional Paper 420-D: 1–109.
- Sohl, N.F. 1963. New gastropod genera from the late Upper Cretaceous of the east Gulf Coast plain. Journal of Paleontology 37: 747–757.
- Sohl, N.F. 1964. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and Prairie Bluff formations. U. S. Geological Survey Professional Paper 331-B: 153–344.
- Sohl, N.F. 1987. Cretaceous gastropods. Contrasts between Tethys and the temperate provinces. Journal of Paleontology 61: 1085–1111.
- Squires, R.L. 1981. Geologic map of Upper Cretaceous Chatsworth Formation, Simi Hills, California (with fossil localities). In: Link, M. H., R. L. Squires, and I. P. Colburn (eds). Simi Hills Cretaceous turbidites, southern California.

- Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles, California: In pocket.
- Squires, R.L. 2003. Turnovers in marine gastropod faunas during the Eocene-Oligocene transition, west coast of the United States. In: Prothero, D. R., L. C. Ivany, and E. A. Nesbitt (eds.). *From Greenhouse to icehouse, the marine Eocene-Oligocene transition*. Columbia University Press, New York: 14–35.
- Squires, R.L., M.H. Link, and I.P. Colburn. 1981. Introduction. In: Link, M.H., R.L. Squires, and I.P. Colburn (eds.). *Simi Hills Cretaceous turbidites, southern California*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles, California: 5–8.
- Squires, R.L. and L.R. Saul. 1981. Dayton Canyon megafossil locality stop. In: Link, M.H., R.L. Squires, and I.P. Colburn (eds.). *Simi Hills Cretaceous turbidites, southern California*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Los Angeles, California: 131–132.
- Stecheson, M.S. 2004. Systematic paleontology of marine gastropods from the Upper Cretaceous Chatsworth Formation, Simi Hills, southern California. California State University Northridge, unpub. M.S. thesis, 142 pp.
- Stephenson, L.W. 1941. The larger invertebrate fossils of the Navarro Group of Texas. The University of Texas Publication 4101, 641 pp.
- Stewart, R.B. 1927. Gabb's California fossil type gastropods. *Proceedings of the Academy of Natural Sciences of Philadelphia* 78: 287–447.
- Stimpson, W. 1865. On certain genera and families of zoophagous gasteropods. *American Journal of Conchology* 1: 55–64.
- Swainson, W. 1831–1832. *Zoological Illustrations*. Vol. 2, Series 2. Baldwin & Cradock and R. Havell, London, pls. 46–91 (unnumbered).
- Toulmin, L.D. 1977. Stratigraphic distribution of Paleocene and Eocene fossils in the eastern Gulf Coast region. *Geological Survey of Alabama Monograph* 13. Two-volume set, 602 pp.
- Wenz, W. 1938. *Gastropoda Teil 1: Allgemeiner Teil und Prosbranchia*. In: Schindewolf, O.H. (ed.). *Handbuch der Paläozoologie*, Vol. 6. Gebrüder Borntraeger, Berlin: 1–1639 [Reprinted 1960–1961].

APPENDIX 1

LOCALITIES OF THE NEW SPECIES

All quadrangles listed below are U. S. Geological Survey, 7.5 minute, topographic maps. For the Chatsworth Formation localities, see Squires (1981) for Simi Hills locations plotted on a topographic base map.

LACMIP 10710 [= CIT loc. 1158], southeast slope of Simi Hills, north bank of Bell Canyon, Chatsworth Formation, Ventura Co., southern California, Calabasas Quadrangle, United States Geological Survey. Age: Late early Campanian. Collectors: W. P. Popenoe, L. R. Saul, J. Alderson, 1935–circa 1990.

LACMIP 10715. [= locs. CIT 1159, UCLA 6965, and CSUN 175], 34°13'12.02"N, 118°40'3.63"W, prominent fossil bed on crest of spur between forks of Dayton Canyon about 122 m east of the Los Angeles–Ventura Co. line, Chatsworth Formation, Dayton Canyon, southeast slope of Simi Hills, Los Angeles Co., California, Calabasas Quadrangle. Age: Middle Campanian. Collectors: R. Durbin, W. P. Popenoe, L. R. Saul, J. Alderson, R. L. Squires, 1935–circa 2000.

LACMIP 42320. Temporary exposure made during construction of the Foothill Transportation Corridor (Toll Road Highway 241), Williams Formation, Pleasants Sandstone Member, elevation 715 ft., 425 m due south of hill 923, west side of Bee Canyon near its mouth, western foothills of Santa Ana Mountains, Orange Co., southern California, El Toro Quadrangle. Age: Early late Campanian. Collector: P. Peck, July 17, 1997.